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FURTHER OBSERVATIONS ON "HILLTOPPING" IN PAPILIO ZELICAON

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In the past I have written two papers in which I set forth the "mating rendezvous" theory to account for the hilltopping habits of certain butterflies. During the ensuing years many things have come to my notice that have sapped my confidence in this theory. After coming to live on Thetis Island in 1965, I found myself in an excellent position to study the habits of *Papilio zelicaon*, which is by far the most notable and persistent hilltopper. The results of my observations here have caused me to abandon the mating rendezvous theory entirely.

Later, in correspondence with Mr. Oakley Shields of San Diego, California, I learned that he was making a detailed study of *P. zelicaon*, with a view to publishing a paper on the hilltopping habits of this species. I felt that, owing to my limited opportunities for research, I could do better by collaborating with Shields, rather than writing up my own findings. He accepted my suggestions for this plan, and for over a year I sent him several long letters detailing my observations. In his paper, "Hilltopping" (196), he referred the reader to my published papers which I had repudiated.

I conceived the idea of crudely marking, and releasing, a few male *P. zelicaon*. I first considered this as a preliminary test, intended mainly to show whether the recovery ratio would be sufficient to warrant a more elaborate program. However, I now feel that the results achieved are worthy of publication.

Thetis Island consists of two ridges running approximately north and south, each about 4 or 5 miles long and reaching 600′ at the highest point. Between these ridges the valley is for a large part below, or barely above, high tide level. In the southern part of this valley an area of about 10 acres is almost flat,

supporting a rank growth of swamp loving herbage, mainly sedges (*Carex* spp.) with a considerable admixture of the water parsley (*Oenanthe sarmentosa*). Undoubtedly, in this swamp most of the *P. zelicaon* population of island feed as larvae.

The land rises quite evenly from the swamp to the summit of the west ridge (Birchall Hill). This hill is close to, and easily seen from, the swamp, and so should provide the most likely place to find hilltopping butterflies. In fact, it is heavily wooded and I have never seen any butterflies there. From the east side of the swamp rises a sheer cliff 100′ high, blocking off all view of the east ridge (Moore Hill). Between this cliff and Moore Hill the land is irregular with many small ridges and valleys. It seems improbable that any insect could find the hill by following land contours, as suggested in my paper on *Oeneis.* Moore Hill is very sparsely wooded at the extreme summit, and on the gradual slope extending northward. It is much frequented by butterflies, chiefly *Papilio zelicaon, P. rutulus,* and *P. eurymedon.*

My system was to clip off the tip of one forewing of butterflies to be released. Those collected on Moore Hill had the left wing clipped, those collected in the swamp the right wing. As an additional check, I clipped the tail from the hind wing opposite to the clipped forewing. Due to the frequency with which Papilios lose the tails by accident, I did not plan to draw any conclusions from insects with missing tails, unless this mark was clearly supported by a clipped forewing. In any event I caught only one individual which had lost the tip of a forewing, other than those which were clearly my released specimens. This one had part of a wing removed leaving a ragged edge, not neatly clipped as in my marked specimens. Both tails were intact. All others, counted as recaptures in the ensuing account, had neatly clipped forewings, and the opposite tail only missing.

In addition to my marking and releasing program, I kept records to ascertain the average time needed to collect, respectively, a male and a female *P. zelicaon,* on the hilltop and in the swamp. I also tried to estimate the number *of P. zelicaon* usually present on the hilltop; as there were very few, this was not difficult. Due to the large area and the large number of butterflies present, no estimate that would be of any value could be made of *P. zelicaon* numbers in the swamp. On the hill I noted, each day that I collected there, (a) the largest number of *P. zelicaon* seen together at one time, and (b) the minimum number

that could have visited the area during my stay. The last figure was arrived at by adding to the number collected any others seen after I had ceased collecting.

The areas which I collect at a given time are decided mainly by mercenary considerations. When *P. rutulus* and *P. eurymedon* are present I collect the hill; when only *P. zelicaon* are available I collect the swamp. As *P. zelicaon* is by a week or two the earliest on the wing of the three species, I commence the season by collecting the swamp, but soon resort to the hill until all species become too worn to be worth any further effort. When the late brood of *P. zelicaon* emerges, the other two species being single brooded, I collect the swamp for the remainder of the season. Thus I did not manage to check the swamp for the possible return there of specimens taken on the hill.

All releases were carried out in my garden. Unfortunately, I do not have any map of a scale that would allow of my calculating exactly the distances involved. The distance to the swamp is a little over a mile; the distance to the hilltop several times farther, a circumstance which can hardly account for the results as follows. The first *P. zelicaon* of the season I collected in the swamp on May 8; these were 2 females, not absolutely fresh. From that date up to May 18, I alternated between the hill and the swamp. The first release from the swamp I made on May 17, but as I did not return to the swamp until June 5, later disclosures will show that I had little opportunity to recapture this one. On June 5, I released two from the swamp, but returned there only one more day, June 7. On that day, I released three from the swamp.

From May 14 to May 25, I was at the hill on alternate days. I released one butterfly on each of the following days: May 16, 18, and 21. On May 25, I released two. On May 18, I recaptured a marked specimen in my garden. I had not yet made that day's release, so this specimen was the one released two days earlier; it had made no attempt to travel anywhere. Following the May 25 releases, I did not get back to the hill for five days. I was then at the hill May 30, June 2, 4, 8, 10, 11, and 13. I released one specimen June 2 and one June 8. On June 10, I recovered one specimen which had been marked and released from the hill; this was the only one retaken while collecting on the hill. I took this one home again, clipped the other wing, and released it; on the two subsequent days I returned to the hill I did not see it. Early flight *P. zelicaon* were now mostly

worn, so I terminated my spring collecting on the hill.

On July 13 I noted second brood *P. zelicaon* on the wing and therefore tried the swamp again. On that day I released four butterflies. I did not get back to the swamp again until July 16, when I recovered one of the July 13 releases. I took this one home, clipped the other wing and released it again, together with the three others captured on the same day (July 16). On my next visit to the swamp, July 18, I recovered two once marked specimens. Both of these, I double marked and released again. On my next and last visit to the swamp, July 21, I recovered one twice marked specimen. On that day, I also recaptured a twice marked specimen at my garden.

In summing up, I think I may be permitted to ignore the six spring brood specimens from the swamp which I released. I made almost no effort to recover these; at that time I supposed that if I did see them again it would be on the hill. Thus we have a recovery rate of one out of seven released from the hill, this one being double marked and not seen again. From the swamp, we have a recovery of three out of seven, these three being double marked and one of them recovered again. In view of the small number of butterflies used, and the much greater distance from the release point to the hill, I can hardly claim that these figures offer convincing evidence to the effect that the butterflies returned more readily to the swamp than to the hill. Still, I think that they can be regarded as suggestive. In any case, this is irrelevant to the theory that I set out to gain evidence on, namely, that butterflies from the swamp had no interest in the hill. I had as much opportunity of recovering the six early releases from the swamp, had they gone to the hill, as I had of recovering the seven released in the summer.

My data for collecting success are also interesting. They show that in the swamp I required 15 minutes to collect a male, and 50 minutes to collect a female. On the hill I required 28 minutes to collect a male, and 5 hours 45 minutes to collect a female. Actually these figures are highly misleading in favor of the hill. On the hill the butterflies are concentrated into about half an acre of level or moderately undulating ground, with a few scattered trees. and only very short grass or mosses between them. The butterflies pass repeatedly over a largely predictable course and so are easily intercepted. In the swamp they are scattered over 10 acres, mostly covered with knee-high saw-edged sedges. This area was at one time cultivated as a market garden, and to keep it drained, it was crisscrossed with

a system of ditches up to two feet deep. Through many years of neglect these ditches have ceased to provide drainage, but many are still effective as traps for unwary butterfly collectors. There is no hope of running through this mess, and no sure way of predicting the course that any butterfly will take, in order to intercept it. Of course, there is no basis on which I can estimate accurately the effect of these handicaps on my collecting success, but as a guess I should say that the opportunity of securing any particular butterfly is ten times as great on the hill. From my records I find that in fact I never saw more than two *P. zelicaon* together on the hill, and it is possible that no more than six in all were there during any of my visits lasting from one to three hours.

It will be realized that to make this collecting at all profitable, I was taking mostly other species, and so it may be supposed that my poor success with *P. zelicaon* was due to such distractions. Actually, since *P. zelicaon* are much easier to net than *P. eurymedon,* and much more in demand among collectors than *P. rutulus,* I always concentrate on any *P. zelicaon* that show up, going for the others when no *P. zelicaon* are in sight. Again, after my elaboration of the difficulties of collecting in the swamp, it may be wondered how I was able to recover so many marked specimens from among the large number scattered over the area. I think the explanation here is that the insects returned, not just to the swamp, but to a particular small area that they had staked out as territory. They may travel over a considerable distance, but as a sort of patrol, continually passing and repassing over the same track. There are in the swamp some patches of slightly higher ground that are dry, and lack the heavy cover of sedges. I soon learned that I attained as much success by staying on these dry patches and trying to intercept any passing insects, as by running all through the sedges and falling into the ditches. It can be seen that if a butterfly returned to its regular patrol, I would collect it again.

There is one evident conclusion to be drawn from these observations. The hilltop is not a permanent attraction for a large part of the *P. zelicaon* population. It is just a good collecting place because it is a very small area in which the presence of a few butterflies can be reliably predicted. When, as is the case here with *P. eurymedon* and *P. rutulus,* the host plants are scattered thinly over a wide area, the hill may be the most productive collecting site. But when, as with *P. zelicaon* here, a large proportion of the available host plants are con-

centrated into a relatively small area, this emergence area provides, on the whole, a better collecting site than does the hill.

The small number of males on the hill could be explained by postulating that these are dominant or successful individuals, which drive all others off. But it is not so easy to account for the almost complete absence of females. In fact, there is no evidence that the hill has any attraction at all for females. I am sure that if I were to mark out half an acre of grassy land anywhere on Thetis Island, and spent five hours there, during the flight season of *P. zelicaon* and while temperatures were favorable to butterfly activity, I could not fail to collect one or more females. In my garden, where there are a fair number of flowers attractive to butterflies, I would quite certainly do much better than that.

When expounding the mating rendezvous theory in my *Oeneis nevadensis* paper, I supposed, with some justification, that *O. nevadensis* was a rather rare insect in the area of my observations. This, added to the fact that females would leave the hilltop immediately after copulation was ended, nicely accounted for my seldom collecting any there. But for a species as common as *P. zelicaon* is on Thetis Island, this theory will not do at all. Every female would have to make at least one visit to the hilltop. Shields, in a letter, has suggested that I do not collect the hill at the right time of day. I have frequently been there in the morning when butterflies were barely starting to move. On the British Columbia coast, where spring nights are always cool, this does not by any means require early rising. There remains the late afternoon. But it is obviously impossible for the insects to predict their time of arrival at the hilltop. One cannot imagine a whole flock of females hiding just down the slope somewhere, waiting to pop up at a given signal. If the collector remains on the spot until mid-afternoon, as I have often done, and no females have shown up, it is safe to predict that there will be very few there that day.

My mating rendezvous theory as set forth in my earlier essays depended on the proposition that the butterflies concerned emerged from the pupae as a few individuals widely scattered. To *P. zelicaon* on Thetis Island, this cannot apply. Plenty of both sexes can be seen at the swamp, and it is quite evident that none of them are headed anywhere in particular. The females are ovipositing and the males are looking for females. I have observed many courtship flights, but seen few actually in copulation. My failure to observe actual pairs may

be largely due to the fact that I would sooner collect the insects than wait to see what they are going to do. But it is probable that most butterfly courtships end abortively simply because females are receptive only for short periods. Whatever the reason for the scarcity of copulating pairs, it obviously cannot be because the females are staving off their suitors until they can get to the hilltop. The advantage accrueing to those that "cheated" would be tremendous. They would avoid waste of time and effort entailed in a long hazardous return journey. Shields' idea that there is an advantage in stabilizing the gene pool is not very convincing. This makes it one of those cases where a habit not beneficial to the individual becomes established because it is of benefit to the population as a whole. I do not wish to wander off here into a long discussion of this concept. It must suffice to say that such a habit must be neutral or at the worst only slightly detrimental in its effect on the individual, otherwise it could not persist long enough to become established in the population.

It would be foolish, of course, to claim that Shields' experiment proved nothing at all. The fact that his butterflies sometimes returned to hills other than those from which they were taken, shows that the homing instinct is not entirely responsible for his recovery of marked specimens. His theory of hilltopping by direct view of the hill is far better than my idea of insects following the ground contours, as set forth in my *Oeneis* paper. But it forces the conclusion that insects cannot reach a hilltop until they come by accident to a point from which they can see it. It could hardly be of much benefit to males to spend their time waiting on a hilltop for females, a large proportion of which would never get there. Shields, as his illustration plainly shows, was able to work on neat little humps sticking out of a nearly level and largely treeless plain. He would almost certainly have obtained different results if he had met with such a situation as pertains here, where very few summits can be seen before you are almost up to them, unless from certain points of vantage. A reasonable supposition would be that the hilltopping instinct becomes dulled under the latter conditions. But could this circumstance almost entirely eradicate an instinct which was of any great advantage to the possessors?

There is a definite relationship between the number of *P. zelicaon* commonly on a given hilltop, and the availability of food plants. On the hill at Wellington, which was much used by *P. rutulus, P. eurymedon,* and *Oeneis nevadensis,* I saw no

more than a dozen *P. zelicaon* in nearly 20 years that I collected there. Yet they were not entirely absent from the surrounding country, and I often found a few larvae on parsley in my garden. Mt. Benson, a very conspicuous lone summit, on most of my visits showed only two or three *P. zelicaon* at the summit. But on Mt. Prevost, which offers similar attractions, there are seldom less than fifteen or twenty. It is true that I have not discovered the source of this comparatively large population of *P. zelicaon* on Mt. Prevost. They could be feeding on *Lomatium,* which occurs plentifully near the summit. In my former paper on hilltopping *P. zelicaon,* I gave as my opinion that the *P. zelicaon* population on Mt. Arrowsmith were feeding on *Lomatium.* But I later came across a hollow near the summit which supported a good stand of *Heracleum lanatum,* a favorite host of *P. zelicaon.* Still, *Lomatium* remains a likely host, and the availability of food plants the most likely theory to account for the variable numbers of butterflies on different hills.

Shields made no attempt whatever to learn whether his virgin females could reach the summit if posed any problems in finding it. He did not quite release them on the summit but he might as well have. Certainly the non-recovery of the mated females is surprising and must prove something. But it does not prove that the virgin females went to the summit in order to find mates, although that would be a reasonable assumption, if there were not so much evidence against it. My guess is that if these reared females had been released out of sight of any hilltop, the virgins would have been recovered close at hand. The mated females, of course, have a strong urge to search for a suitable host plant, and this would account for their moving quickly away from the scene of their release.

If butterflies commonly attempted to reach hilltops from any distance, one would expect while collecting to note among all butterflies a cross country movement in a particular direction. Instead, nearly all of them tend to fly low, and, if they do not stay in the same place, they travel in such directions as will not force them to fly over or through trees. This is very noticeable when collecting on roads, when it is very easy to intercept one's quarry, or follow it for long distances, because of its reluctance to leave the nice clear track.

In the swamp here, female *P. zelicaon* are usually seen travelling slowly, with a rather hovering flight, just above the herbage, frequently dropping out of sight therein. Males patrol, also just above the herbage, evidently on the lookout for females. Since this quest often brings them down into the sedges, both

sexes exhibit a characteristic damage to their wings, consisting of numerous small cuts and nicks inflicted by the saw edges of the sedges. The reader will have remarked that I collected the summer flight for only about a week. The reason is that these sedge inflicted abrasions become so prevalent after a short time that the butterflies are not worth collecting any longer. On the hill, this type of damage did not show up at all, and I was able to take saleable specimens for over a month. This again provides evidence that the small numbers of *P. zelicaon* on the hill, in contrast to those in the swamp, are almost certainly due to the fact that no butterflies from the swamp ever get so far. Somewhere close to the hill there must be small patches of a suitable host plant, not associated with sedges.

There is a vast difference between my experience with Rhopolocera in general, and those of Shields and others, who list a large proportion of available species as hilltoppers. Part of this discrepancy, as I have already suggested, may be due to differences in the general aspect of the terrain. But I still find it very difficult to accept the idea of possible hilltopping, under any circumstances, of many species. Among the Lycaenidae, for instance, there are many species that I never see more than 50 yards away from a good stand of the appropriate host plant.

Mt. Benson offers a particularly good opportunity for assessing the hilltopping proclivities of butterflies. I have visited this summit an estimated 60 times during the past 24 years. On each visit I walk about four miles from an elevation of about 2000′ to the summit at 3300′. On this hike, I have collected 30 species of butterflies, of which one, *P. zelicaon,* is almost always taken at the summit only, and two others, *Vanessa cardui* and *V. atalanta,* tend to be at the summit more often than elsewhere. The other 27 species are definitely not more numerous at the summit, and in many instances are less so. I have not included *Papilio rutulus* and *P. eurymedon* in my count of species, although I have taken both species infrequently in the first part of the climb. To have included them would have given the impression that I do not consider them to be hilltoppers, which they most definitely are. Their absence from Mt. Benson summit seems to be due to the fact that they have a strictly limited altitudinal range. It is interesting to note that this aversion to going beyond a certain height (about 2500′ on Vancouver Island) completely inhibits their hilltopping instinct.

One of the commonest butterflies on Mt. Benson is *Oeneis nevadensis.* Females are not commonly seen at the summit.

Males are as plentiful on every little hump of rock or subsidiary peak, as at the summit. This circumstance does not support either the theory of Shields (and others) to the effect that the butterflies head for a conspicuous object on the horizon, or my theory of insects following ground contours. It seems much more probable, with *O. nevadensis* at any rate, that the butterflies have never been so far away from these sites selected as territories that they cannot easily blunder on them by chance. On my hill at Wellington, the illusion of hilltopping was imparted because there were no acceptable rock humps except at the top. Lately I have come across *O. nevadensis* males using as territories patches of bare sandstone showing no eminence above the plain. Evidently the exposed rock has a considerable influence on their choice. In the only occasion on which I have been able to observe an unconfined female *O. nevadensis* ovipositing, the act took place right on the summit of the Wellington hill, again supporting my theory that the insects do not go far to find their territories.

Several males may occupy the same territory. The very sparse population of *O. nevadensis* on my Wellington hill made it easy to suppose that only one male could remain on a site. Actually, when an insect has kept a territory to itself for a short time, any other male arriving will be accosted and perhaps driven off. But the principle, now well known to zoologists, that a stimulus applied too often over a short time, will produce a progressively weakening reaction, applies in this case. When several males are continually invading a territory, they become accustomed to one another. They then accost each other only briefly, and do not fight. This rule applies to other territory holding butterflies, including the Papilio species.

Limenitis lorquini provides another good example of a territory-holding species. But the reasons governing this butterfly's choice of sites are not nearly so evident as is the case with others that I have dealt with. After observing a number I have noticed a similarity. Most consist of a bare or grassy patch on a south facing slope, with dense shrubbery or trees at the upper end. The butterflies settle frequently on these shrubs or trees at varying heights from the ground. It is evident that a warm air current will travel up the slope to be intercepted by the trees at the top. I must make it clear that I am not claiming that most specimens of *L. lorquini* are found in these situations. Large numbers are found in what may be makeshift territories, or may not be territories at all, or the butterflies may be visiting

water, or wet spots to obtain moisture. But when a certain spot is consistently used by *L. lorquini* males, when it is always reoccupied shortly after being cleared off by the collector, then such a spot will usually fit the above description.

In recent years, the territory holding-habit has come in for much attention, and it has been shown that it exists in some degree in a very large proportion of animal species. Many experiments with different animals have shown that they possess an uncanny ability to return to their home territory, even over a completely unfamiliar course. But it has been shown that this ability is not inborn, nor is it necessarily its natal area which the animal knows as home. An awareness of the territory to be known as home must become imprinted on the animal, and this process may take a certain amount of time.

Among animals, winged insects must be particularly likely to be carried against their will by wind; moreover, their eyes are not fitted for making out fine detail. It is reasonable to suppose that insects may have some difficulty in remaining on any selected spot long enough to become familiar with it, so as to be able to return from a distance should such a necessity arise. Conspicuous features of the terrain, such as a hilltop, would help a lot in obviating this difficulty. Add to this the advantages of the heat holding qualities of rocks, warm updrafts, and exposure to the sun early in the day, and I think we have a fairly good theory to account for the selecting as territories of sites possessing the several features described above. But I still remain convinced that the main factor influencing the selection of a territory is its proximity to the spot where the insect commenced its adult life.

By accepting the idea that insects make no great effort to find a hilltop, but merely use one as a territory if they happen to blunder on to it, or see it, the objections outlined above are avoided; in contradistinction we need not suppose that hilltopping can become a blind instinct spread through the population by natural selection. This would account for some insects using hilltops which do not appear to offer many favorable features.

Over unusually favorable terrain, such as that so well depicted in Shields' illustration, insects might go to a hill by sight from quite a distance. Shields mentions particularly a marked butterfly which reached a hilltop concealed from the release point by a ridge. But to accomplish this feat the insect required nine days. Surely, in wandering at random for that length of time,

it is not surprising that it got into a position from which it could see the hill.

The study of congregations of insects, with a view to proving that a mating rendezvous is involved, could easily be approached with too single-minded an attitude. When the primary reason for the congregation is obvious, as when certain species of beetles appear in great numbers on a fallen tree, we do not express any surprise on noting the large number of pairs in copulation. We know that, in order to reproduce, these beetles must find a tree of their correct host species in a condition that makes it vulnerable to their attack. We do not dwell on the fact that the male beetles can have no interest in the tree itself, or we may suppose that it is emanations from the female beetles, rather than the tree, which attracts the males. The last may be the true explanation but that does not alter the fact that a knowledge of the beetles' life history is necessary in order to evaluate the true reason for the congregation.

To sum up, I consider that hilltopping is usually an aspect of territorial behavior. With many insects, hilltops provide a preferred site for territories, and will be used for that purpose when they can easily be reached from the point where the insect commences its adult life. When a number of individuals of a single species reach the same hilltop, they can manage by splitting it up into small territories, or by sharing a territory. Explanations to account for territorial behavior can be a very involved subject. Shields, citing various authors, mentions: (1) decreased chances of mass predation by a few predators, (2) less time spent in intraspecific aggression, (3) increased frequency of male-female encounters, and (4) decreased interference to courting and mating pairs by other males. Therefore, hilltopping can be said to facilitate mating to whatever extent territorial behavior in general facilitates mating.

The above discussion deals with a particular aspect of hilltopping. Obviously, there are other reasons why insects, in congregations or singly, are to be found on hilltops. Apart from species that require arctic or subarctic conditions, which may be found on mountain tops, there are some that prefer a hilltop habitat for less obvious reasons. Often they are found on hills which are not high enough to provide alpine conditions, but since they are not found in the surrounding area, they cannot be called hilltoppers. On Vancouver Id., three species of Arctiid moths provide good examples of such behavior. They

are *Alypia ridingsi* Couper, *A. langtoni* Grt. and *Leptarctica californiae* Wlk.

Lastly there is the strange fact that hilltops are always likely places to turn up unusual locality records. I will not venture any theory to explain this phenomenon. From a number of my own interesting hilltop captures, both in the Lepidoptera and the Coleoptera, I will select the most remarkable as an example. I refer to the taking, on Mt. Arrowsmith in August of 1966, of a specimen of *Pieris sisymbrii Bdv.* The specimen was sent to Dr. dos Passos for positive identification. The species was not previously known to exist anywhere west of the coastal mountains in British Columbia. This individual had enough of the wing area torn off, on one side only, to seriously impede its flying ability.

LIST OF RHOPALOCERA SPECIES COLLECTED ON MT. BENSON

Subspecific names omitted

Papilio zelicaon
Parnassius clodius
Colias occidentalis
Neophasia menapia
Cercyonis alope
Oeneis nevadensis
Speyeria hydaspe
Boloria epithore
Polygonia faunus
P. ____ zephyrus
Nymphalis milberti
Vanessa atalanta
V. ____ cardui
Limenitis lorquini
Strymon melinus
S. ____ californicus
Incisalia iroides
I. ____ fotis
I. ____ eryphon
Lycaena mariposa
L. ____ helloides
Everes amyntula
Plebeius melissa
P. ____ icarioides
Glaucopsyche lygdamus
Thorybes pylades
Pyrgus ruralis
Erynnis icelus
Hesperia harpalus
Ochlodes sylvanoides